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ZOIC MAXIMA, OR PERIODS OF NUMERICAL VARIATIONS IN ANIMALS.

BY L. P. GRATACAP.

NO feature, perhaps, in his geological and field study affords the palæontologist more interesting material for his speculations on the conditions of the past, in its zoölogical bearings, than the irregular distribution of organic remains in the fossil-bearing rocks. Not only in the same geological horizon will he find striking variations in the abundance in which the fossils occur, as he passes from layer to layer of contiguous and often of the same beds, but he soon discovers the important fact that localities are distinguished by peculiar fossils, that a limited range circumscribes the lateral as well as the vertical diffusion of a species, as far as regards *numerical concentration*, and that again points or limited areas present, in overflowing numbers, representatives of an organism which, generally occurring throughout a wide geographical range, are at these points illustrated in crowded and exuberant colonies.

The well-known *fish beds*, located by Newberry and Worthen in the Lower Carboniferous limestone of Illinois, are examples of the first case mentioned, the remarkable localization of forms in Wisconsin, instanced by Chamberlain and by him denominated as evidences of "colonial tendencies," is an example of the second, as also to some extent, though these are perhaps in the main instances of a different class of facts, the faunal stations of Williams so admirably depicted in the papers on the "Fossil Faunas of the Upper Devonian,"[1] while the interrupted display of the same species in the same line of outcrop in respect to the relative numbers of specimens to be seen or their local disappearance when the area examined has any considerable extent, corresponding to a beach line of miles in length, illustrates the third class of facts which we refer to, as the diminishment westward from Genesee of Pentamerus in the Clinton rocks of New York.

Associated with these familiar facts is the closely related one of the contrasted size of the same fossil species in different parts of the same formation, a difference of size not always explicable on the mere assumption of favorable or unfavorable environment, of which perhaps the Spergen Hill fossils afford a very pertinent illustration, for, as pointed out by Professor Whitfield,[1] the diminutive fossils of some molluscous species found at Spergen hill became, at Paynter's hill, a little over a mile west of the former locality, much larger, while the Bellerophon and Euomphalus of the Ellettsville, Ind., beds, greatly exceed in size the same species from Spergen hill, and in a less striking way collectors have become familiar with certain localities where certain fossils assume an unusual or handsome size contrasting with their depauperate appearance elsewhere.

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[1] Bulletin U. S. Geol. Surv., No. 3.

A great deal of instructive and careful study has been expended in recent years, since the advance of research has made naturalists better acquainted with the oscillatory character of faunal populations, upon the perplexing question of the contemporaneity and succession of fossil faunas, and Barrande, Etheridge, Hall, Hull and Gosselet abroad, and Williams, Walcott, Call, Clarke and Matthews at home, have pointed out some of the details of their results in this investigation, and have already familiarized the scientific world with the important conception that varietal faunas or modification of a central or controlling animal facies, or even sharply contrasted zoölogical aggregations of species may belong to the same epoch and be laid down in the neighborhood of each other on the same oceanic or lake flooring.

Our intention here was not to discuss the variations of specific forms in the fossil-bearing rocks as throwing light upon the synchronous existence of different faunas, their succession, retreat, reappearance and fusion. It is undoubted that these assumptions explain and are indeed the chief explanations to be offered for the varying character of near-lying fossil groups; but we wish to urge upon the consideration of palæontologists the necessity of allowing—as far as regards the instances of fossil distribution cited above, viz., the greater or less prevalence at near horizons or beds or along the horizontal extension of the same bed of the same fauna or species—for those irregularities of production of life, which cause in our present seas different years to become distinguished for a phenomenal abundance of certain forms, as others to claim a distinction for the abnormal decrease or disappearance of the same forms over the same geographical area. Thus a given spot on a coast line, always yielding a particular species, may in one season become the abode of numbers of these same animals out of all proportion to its ordinary *census of occupation*, and in another season pass, by an abrupt change or perhaps through a series of less violent alternations, to a condition of comparative or actual denudation of these residents. The work of the Fish Commission has made us familiar with facts of much wider import, when large sections of the oceanic basin have become depopulated. This latter case appears to be catastrophic in its causes, but comes within the scope of our suggestion as to the fluctuating fertility of a species. And the fact becomes sometimes apparent that in a restricted region commanding a more or less fixed supply of nourishment the size of the animals will increase in the years of decreased fertility, and correspondingly diminish in the seasons of enhanced productivity, a relation not unnatural.

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[1] Bulletin Amer. Mus. Nat. Hist., Vol. I, No. 3.

To what extent we may parallelize these two classes of facts, the one dealing with the changing abundance of fossil shells or remains, either vertically or horizontally distributed in beds of the same age, and the other exhibiting the varying numbers, in separated seasons, of contemporaneous animals along our seaboards, or in our fresh-water lakes, or even, so far as we can determine, in the pelagic areas, is not at first, or in all cases equally easy to determine. But it is possible to review some considerations bearing upon the general question.

The observations which may be adduced as bearing on this question are necessarily widely scattered, and when found are for the most part concerned with those forms of life which subserve some industrial or economic uses, or with those in close relation with the former, as, for instance, the recorded irruptions of starfishes (*Asterias forbesii*) and "drills" (*Urosalpinx cinerea*) in different years upon our oyster beds. In classifying, however, the efficient causes which effect these variations of animal populousness, without entrenching upon ground more or less speculative, we may say that the changing abundance of animal forms in different years or localities arises mainly from:

1st. Opportunity for or difficulty in obtaining fecundation.

2d. Constitution, rate of growth, habits, etc., of organism.

3d. Character of habitat in relation to bottom.

4th. Phenomenal influences, as cataclysms, poisoned or heated waters, storms, destruction by enemies.

I. Opportunity for or difficulty in obtaining fecundation.—That this has an important influence in securing a great or small representation of the marine animals in modern seas is unquestioned, though it is always, of course, a variable function of the more or less rapid and safe methods nature uses for their multiplication. Dr. Brooks says :[1] "The most critical time in the life of the American oyster is undoubtedly the time when the egg is discharged into the water to be fertilized, for the chance that each egg which floats out into the ocean to shift for itself will immediately meet with a male cell, is very slight, and it is essential that the egg should be fertilized very quickly, for the unfertilized egg is destroyed by the sea water in a very short time."

Tryon has suggested that the swimming species of Cephalopoda may experience some difficulty in effecting sexual union,[2] and the observations of Steenstrup upon the many different ways adopted in this group of Mollusca for fertilization, justify the inference that under unfavorable circumstances individuals of the same group may not encounter each other, and the chances for the fruitage of the same genera be diminished in exact ratio to the opposite plan pursued by its congeners for their fecundation. With some of the gastropods sexual union is effected directly, and no danger is incurred from the exigencies of the unprotected female ovum searching for the spermatic vesicles in the water. This establishes a safeguard which favors the multiplication of those prosobranchiates which possess it, but in other groups (Trochus, Scutibranchs, Cyclobranchs) the male elements are discharged into the water, and are then taken into the uterus. This introduces a risk which must increase or lessen according to the presence or absence of predatory fishes who devour the spat, the favorable stillness of the water or its temperature, or chemical condition, which if abnormal would destroy the germs.

Professor Morse[3] has described the difficulty, arising at a rocky point at Eastport, Maine, of the larger males of *Buccinum undatum* securing contact with the diminutive females secreted in the narrow apertures and crevices of the ledge, a state of things which at first would have a tendency to reduce the number of the individuals until a sufficient number of small males were evolved to maintain the most complete generative activity, though this very contraction of size might diminish vitality, disarrange the seminal function and result in sterility.

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[1] Bull. U. S. National Mus., No. 27, p. 210.

[2] Manual of Conchology, Vol. 1, p. 42.

[3] Proc. Boston Soc. Nat. Hist., Vol. XVIII, p. 284.

The orders of Cladocera, Copepoda and Ostracoda will, in this respect, be favorably placed in comparison with other crustacean groups, as in these tribes fertilization of the female lasts during her lifetime, or at least a season, and in some cases the young females are born fertilized from the impregnated mother. Thus favorable conditions with these groups gain a predominating influence, as they fortify and assist an already preëxistent advantageous arrangement for security of fecundation.

Amongst fishes advantage will be given to those whose spawning season is most extended, as with cod, with which, according to the observations of Professor Sars, it extends over nine consecutive months, "a period exceeding that required by any other species of which we have any knowledge."[1] These are not only more likely, with equal vitality, to produce a larger number of individuals, but they are absolutely favored, by the greater extension of time, to escape variable inimical circumstances, which latter, being limited in duration, might, if coincident with the shorter period of other fishes, greatly impair the prospects of successful fecundation. The longer period of the cod renders its partial or entire escape from such disasters more probable. The spawning season for an individual of shad, salmon, or white fish is only a few days. But the likelihood of impregnation seems to be diminished on spawning grounds where strong currents are found, or during storms, as immense numbers of the eggs are driven on the shores, or are so diffused and distributed as not to meet the milt of the male, and as the egg of the cod quickly loses its vitality, great numbers perish. Under very favorable circumstances such conditions for impregnation might prevail as would result in an enormous excess of individuals produced, whilst an opposite state of affairs would reduce the production to a minimum. Again, an insufficient supply of males would greatly modify the results of fecundation, as the extraordinary fertility in eggs of the female amongst fish necessitates the presence of several males to accomplish their fertilization. Eggs of fish which are of such a gravity as not to rise to the surface, unlike those of the cod and mackerel, come less in contact with the destructive agencies of the surface, and increase their likelihood of fecundation by the longer possible period thus secured for a greater number.

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[1] Bull. U. S. Fish Commission, Part v.

Such fish as spawn in rivers or in the later seasons, as early summer, may be in some instances, or most, more likely to perpetuate a greater number of offspring than their congeners whose eggs in the ocean are exposed to greater risks of destruction or at seasons when storms are prevalent, though this consideration is again modified by the possible presence in either case of more numerous enemies.

II. Constitution, rate of growth, habits, etc., of an organism.—It is obvious that conditions favorable for the preservation and maturization of individuals will prevail when these conditions harmonize with the habit and life-history of the organism, and that the reverse will ensue when they do not, and other things being equal we may expect those species to predominate at a locality whose habits, life-history, etc., are either best adapted to the conditions of that locality over its competitors, or are of such a character as to withstand conditions which, generally unfavorable to all forms of life, are met by it with better safeguards and greater resistance.

Under unfavorable conditions the longer time in which the young of a marine shell are free before attachment, the less chance for a survival of a great number, and at such a time a selection would be effected in favor of those species whose spat most quickly came to rest, and these would subsequently become phenomenally frequent.

Again, the power of an organism to endure change of temperature, as compared with others less able to survive variation in this respect, obviously works in its favor, and may lead to an *apparent* excess of individuals. As Semper says,[1] "a small fall in temperature may be as injurious to one animal as a great fall to another, while a third species may be wholly unaffected by either." Möbius has designated animals under this regard as *eurythermal* and *stenothermal*, as they are qualified to endure great or small variations of temperature. This will also have an important influence on size, as Möbius has shown that the same species of mollusk living on the coast of Greenland or in the Baltic was in the former case large, in the latter dwarfed, and he attributed it to the variable temperature in the latter locality. Rate of growth as it is rapid or slow, continuous or periodic, will affect the numerical display of a species. Thus *Pecten irradians* grows very quickly, stops in winter, beginning again when the scallops are one year old, and on the whole this irregularity may be regarded as tending to diminish numbers. Power of locomotion again assists its possessors to escape from unfavorable surroundings or from enemies. Swarming or migratory habits, as with lobsters, affect the numerical proportion of the species at a given point in certain seasons, but probably has little influence on the fertility or abundance of individuals. Those animals, as crustaceans, which cast their integuments, are exposed to accidents during their exposed period, and should they then be subjected to especially destructive influences would suffer great numerical depletion.

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[1] Animal Life, p. 105.

III. Character of habitat in relation to bottom, temperature, depth, isolation, salinity and supply of food.—The overwhelming importance of these very variable factors upon the numerical exhibit of a species is most evident, and has, from many points of view, been emphasized by naturalists. Thus the nature of the bottom exercises a predisposing selective influence upon molluscous distribution. It is well known that oysters are killed in the mud, that the round clam affects sandy and muddy shores, the edible muscle flourishes in a variety of positions and surroundings, that the Purpura loves rocky headlands, and so on indefinitely. The temperature of the water exercises an accelerating or retarding influence upon the growth and spawning of both shells and crustaceans according to their nature in this respect, and the increase or decrease of heat. In the matter of living at different depths, animals vary extremely, and the sudden settling of a shore or even rapid secular change would tend to destroy the classes of shallow-water loving organisms. Isolation permits close interbreeding, subjects the species to more uniform conditions, and if it diminishes the volume of water seriously modifies the size, as shown with Lymnæa by Semper and Hilger, while of course it induces peculiarities of local development. Salinity varies in sea water and enclosed areas of the ocean, and distinctly modifies the abundance of animal life. The character of the supply of food and its abundance is an obvious element of great importance in the production of sea animals.

IV. Phenomenal influences, as cataclysms, poisoned or heated waters, storms, shocks, destruction by enemies.—It is enough to mention these to suggest their frequent occurrence. But the effect of these in geological time has been, doubtless in some case, to produce deposits of animal forms in sudden abundance, as when a fauna by their action has almost simultaneously disappeared. Thus Dr. Newberry has suggested that the fish beds of Illinois afford evidence of a wholesale destruction of fish life, possibly through submarine explosion, diffusion of poisoned vapors, etc., while the phenomenal disappearance of animal life from the Atlantic, as shown by the observations of the Fish Commission in 1881, is a modern instance of a widely extended catastrophic obliteration of animal forms.

Zoic Maxima.—It is evident that if all the above conditions were favorably conjoined for some reasons, in accordance with the needs of any special organism or any group of organisms, that these would attain probably an unusual fertility, and that if passing such a climax as this the succeeding years would develop conditions in the same way, as strikingly unfavorable, we would have in the marine deposits, accumulated during these years, two contrasted beds of respectively rich and barren contents connected or graded into each other by intervening beds of diminishing productivity in shell remains. But if after a period of phenomenal activity and success in the production of forms such as instanced, a disaster, such as those we have suggested under the fourth heading, took place, then we would have a bed gradually reached through lower beds of increasing numerical strength until it crowned the series as a climacteric to be succeeded by later layers quite devoid of animal remains.

These periods, when all the conditions are most favorable for animal multiplication, we designate as Zoic Maxima; and as they are in accordance with the requirements of the greatest number of specific forms we call them Pan-zoic Maxima; or as they are so combined as to exert a selective influence, permitting the preponderance of one or a few species, or directly contributing to the propagation of this one species both in numbers and in size, we call them Sol-zoic Maxima.

It is certainly true and known that such Zoic Maxima, both in their general and restricted manifestations, are known in our contemporaneous faunas. It is probable that the varying abundance of fossil remains in the beds of fossil-bearing rocks are due to similar causes.